University of Kansas Publications
Museum of Natural History

Volume 12, No. 8, pp. 347-362, 10 figs.
October 1, 1962

Teeth of Edestid Sharks

BY

THEODORE H. EATON, JR.

University of Kansas
Lawrence
1962

University of Kansas Publications, Museum of Natural History

Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 12, No. 8, pp. 347-362, 10 figs.
Published October 1, 1962

University of Kansas
Lawrence, Kansas

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1962

29-4226

Teeth of Edestid Sharks

BY

THEODORE H. EATON, JR.

The Edestidae are a family of Paleozoic sharks, known from rocks of Mississippian to Late Permian age, and characterized by a series of median, symphysial teeth of specialized structure. In *Edestus* such teeth occur in both the upper and the lower jaw, but in other genera it is not yet certain whether those of the two jaws are alike. Several genera have been described from single sets of symphysial teeth, presumably belonging to the lower jaw. Sets of lateral teeth of the lower jaw are known in *Campodus* (*Agassizodus*), associated with the symphysial series. In this genus the structure and arrangement of the symphysial series are not radically different from those of the lateral teeth, but in other genera the symphysials are increasingly modified until, in the Permian *Helicoprion*, an extraordinary spiral band of teeth is formed in the symphysis, the function and position of which have been difficult to determine.

Moy-Thomas (1939) divided the Chondrichthyes into two orders, presumed to represent divergent evolutionary lines, on the basis of tooth structures. One, the Bradyodonti (proposed on different grounds by Woodward, 1921), comprised sharks in which the outer layer of the tooth was of hard dentine containing vertical tubules, but without enamel. Moy-Thomas included in the Bradyodonti the Edestidae and Orodontidae, as well as the Petalodontidae, Cochliodontidae, Psammodontidae and Copodontidae (following Woodward), and he added also the Holocephali. Radinsky (1961) investigated tooth histology in Chondrichthyes, and concluded that the order Bradyodonti is probably artificial, that it cannot be defined by the character of "tubular dentine," and that it should not include Edestidae and Orodontidae. He suggests that the name Bradyodonti be retained, however, for the four families designated by Woodward, "on the basis of slowness of tooth replacement," and that the Bradyodonti be "included with chimaeroids under the term Holocephali . . . Until further evidence is found, it is suggested that the edestids be kept as a separate group, related to hybodonts and heterodonts."

Accepting this idea, we nevertheless meet other difficulties in attempting to understand the Edestidae. Little material other than teeth has been found, but probably certain fin-spines and denticles known under other names will eventually be associated with Edestid

teeth. Lateral and symphysial teeth are seldom found in association with each other, and this circumstance has resulted in confusion of some generic names, as described on pages 350 and 351. A new species of *Fadenia*, based on symphysial teeth, is named and described farther on. The arrangement of the symphysial teeth in this family has been the subject of prolonged controversy, now diminished as a result of the general agreement of authors that these teeth belong in the median line of the lower jaw, and that the upper jaw also bears a series of symphysial teeth. But the direction in which the series are oriented, and the manner in which the *Helicoprion* spiral evolved from the simpler patterns seen in other genera, have not been demonstrated satisfactorily. A solution to these problems is proposed in the last part of this paper. The illustrations were prepared by Merton C. Bowman.

Obruchev (1953), in a monograph devoted primarily to the work and discoveries of A. P. Karpinsky, reviewed much of the history of investigations of the Edestidae. Without adding conclusions or data of his own, he compiled most of the information so far published, with excerpts from unpublished correspondence of Karpinsky and others, in a useful summary of the subject. As this publication, in Russian, may not be conveniently available to many students in the United States, several figures have been redrawn from it for the present paper. The value of Obruchev's work seems to be as a historical source rather than a contribution of new evidence or interpretations.

Status of Campodus and Agassizodus

DeKoninck (1844:618) described the genus *Campodus* on the basis of scattered teeth (*C. agassizianus*) found in "calcareous nodules in the black shale of Chokier, underneath the coal formation" (translated), in the Lower Westphalian or Namurian beds of Belgium, early Pennsylvanian in age. The teeth are weakly arched, oblong, up to about 15 mm. in length, and surmounted by a small series of hard, shiny tubercles, each of which is also oblong but with its axis transverse to that of the tooth. The tubercles themselves bear minute ridges, and similar ridges are seen also in the depressions between the tubercles. Other, much larger ridged teeth were intermingled with these, but were referred by DeKoninck to *Orodus ramosus* Agassiz.

Teeth apparently congeneric with the latter were described from the Mississippian of Illinois by Newberry and Worthen (1870:358), as *O. corrugatus*. The same authors also described, but with some

hesitation regarding its generic distinctness, a series of teeth from the Pennsylvanian of Illinois under the name *Lophodus variabilis* (1870:360). In 1875, however, St. John and Worthen, finding that the name *Lophodus* was preoccupied, proposed the genus *Agassizodus* for *L. variabilis,* and included in the same genus *O. corrugatus* and two other species. These authors illustrated a large mandible of *A. variabilis* bearing numerous rows of teeth (St. John and Worthen, 1875, pl. 8, fig. 1). The middle row contains the largest teeth, but towards both ends of the mandible the teeth become much reduced and show a form much like those named *Campodus* by DeKoninck; the specimen was found in Upper Pennsylvanian beds near Osage, Kansas.

Lohest (1884) examined DeKoninck's specimens of *Campodus agassizianus,* obtained more material from the beds at Chokier, and was authorized by DeKoninck to continue the description of the genus. His figures show teeth closely comparable to the American *Agassizodus,* and an almost complete intergradation between these and the specimens of DeKoninck's *Campodus.* There can be little doubt that the teeth figured by Lohest all belong to one species, if not to one individual. Lohest concluded that the name *Campodus* should apply both to DeKoninck's *C. agassizianus* and to the American species of *Agassizodus.* After study of the figures published by the authors mentioned, and by Eastman (1902, 1903) and other more recent writers, as well as of the material in the collection of the Museum of Natural History, University of Kansas, I am convinced that Lohest was correct, and shall therefore refer to species that have been described under the name *Agassizodus* as *Campodus.* Most authors subsequent to Lohest (except Eastman) have continued to recognize *Agassizodus,* however. Probably this is because the smallest teeth in the jaws, when present, have not been compared in detail with DeKoninck's series, or have not been illustrated with sufficient care to enable others to notice the resemblance.

Nielsen (1932), in a review of the literature on Edestid teeth, justified the name *Agassizodus* on the ground that symphysial teeth show generic characters better than lateral teeth, and that whereas symphysials were known for the American *Agassizodus,* none were as yet available for *Campodus.* This view disregards Lohest's evidence, which appears satisfactory, that there was no basis for separating the two genera in the first place, inasmuch as the broad range of variation of the lateral teeth in both encompasses the same characters. Neither *Campodus* nor *Agassizodus* was founded upon symphysial teeth.

Symphysial teeth of *Campodus variabilis* have been figured by Eastman (1902, pl. 1, 2, 3; 1903, pl. 1). Isolated symphysial teeth of the same species are in the KU collection (Fig. 1). St. John and Worthen (1875, pl. 8, fig. 24) illustrated an imperfect symphysial tooth of more massive form, with a thicker median knob,

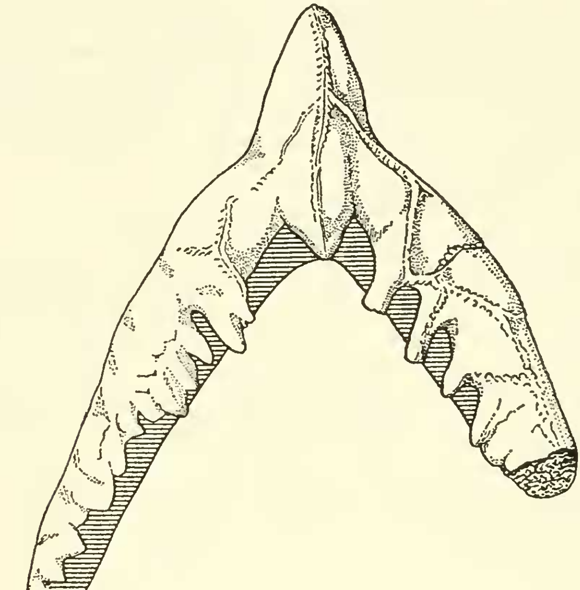

FIG. 1.—*Campodus variabilis,* symphysial tooth, posterior aspect. KU 1056, × 1.5.

as "*A.*" *corrugatus.* Nielsen (1932:37) doubted that this could belong to the same genus as the lateral teeth so named, but I see no reason to question it.

A New Species of Fadenia

Among the Lower Permian fishes described by Nielsen (1932) from East Greenland were two species of Edestidae, both represented by an abundance of teeth. One he named *Agassizodus gronlandicus* (here regarded as *Campodus*), and the other *Fadenia*

crenulata. In the latter the symphysial teeth are much more massive, both in the crown and in the steep lateral flanges, than those of *Campodus.* The median peaks are blunt, the anterior and posterior edges of the flanges of each tooth are crenulated, the anterior most strongly, and the lateral surfaces of the flanges are flattened and bear horizontal wrinkles (Nielsen, 1932, pl. 4, figs. 1, 2, 9-12).

Nielsen's characterization of *Fadenia* is quoted: "Symphysial teeth (at least of one jaw) disposed in an unpaired row, not fused with each other, and of a bilaterally symmetrical shape. Crown of the symphysial teeth as normally in the Edestids developed in such a way that its right and left halves meet in an acute angle forming a pronounced rostro-caudal edge. . . . Crown of the symphysial teeth at the median plane broader than one half of the length, with the labial margin much and the lingual margin only slightly folded, and with a sculpture of plicae, which, possibly on account of wear, are much less distinct on the highest median than on the lowest lateral parts. . . ." He describes and figures both the symphysial and the lateral teeth, but inasmuch as no lateral teeth accompany the specimens to be described here, only the symphysials are pertinent. Nielsen also remarks that there is less difference between the lateral and symphysial teeth of *Fadenia* than between those of any other edestid, and this genus must therefore be the most primitive one known in the family. The type species, *F. crenulata,* was found in Pennsylvanian limestone, Cape Stosch, East Greenland.

Two specimens in the Museum of Natural History, University of Kansas, have characters that place them in *Fadenia* rather than *Campodus,* and are described here as

Fadenia gigas new species

Type: Two symphysial teeth in place on a block of osteodentine (Fig. 2); No. 1023, Museum of Natural History, The University of Kansas; found 4 feet below top of Cherokee shale (Lexington coal), Lower Pennsylvanian, at Lucas, Henry County, Missouri. There is no information as to the collector or date.

Diagnosis: The teeth resemble those of *F. crenulata* in proportions and shape, in having a rostro-caudal edge in the median line, and in a sculpturing of plicae on the lateral surfaces. But they differ in having both the labial and the lingual margins much folded, and in being of far greater size (*gigas,* Greek, giant). The height of the more complete tooth is 79 mm., not including a small part of the tip that is missing; its anteroposterior breadth in the median plane is 45 mm. These measurements contrast with 23 and 15.5 mm., respectively, as determined from Nielsen's fig. 12 on plate 4.

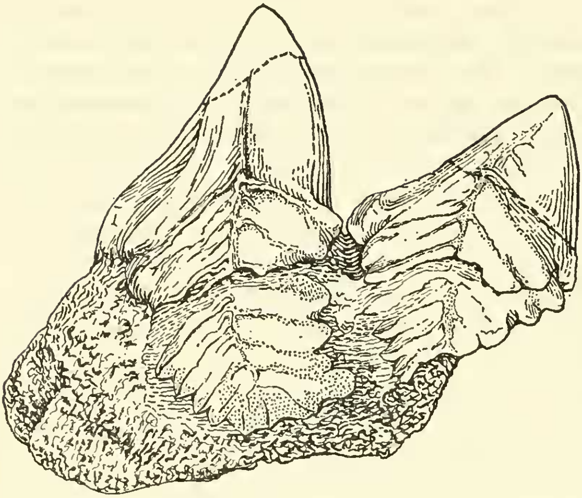

FIG. 2.—*Fadenia gigas,* new species, symphysial teeth, right side. KU 1023, × 0.65.

Referred specimen: KU 865, consisting of two symphysial teeth, attached to a block of osteodentine, that are smaller than those of the type. The folds of the anterior and posterior margins are farther apart and less numerous than in the type, but the general shape and the pattern of plicae on the surface closely resemble it. There is no information on the source of this specimen, but its form, color, and mode of preservation strongly suggest that it came from the same horizon as the type. Probably the specimens pertain to different regions of the symphysial series, but there is no evidence to show whether the series formed a simple arch or a spiral; the former, to judge from Nielsen's *F. crenulata,* is more probable. The shark from which they came must have been large, perhaps four or five meters in length, to accommodate a series of such massive teeth and their counterparts in the opposing jaw.

Position and Evolution of the Symphysial Teeth

Neither the orientation of the *Helicoprion* spiral in the animal that carried it, nor the relationship of this curious device to the symphysial series in other edestid sharks seems to have been stated convincingly. In the more generalized members of the family, *Campodus* and *Fadenia,* it is clear that in the lower jaw, at least, a median row of teeth curved forward and outward, that they represented a growth series, and that the more lateral teeth were also arranged in series that curved up and out over the occlusal surface of the mandible. Whether these also were growth series is not entirely clear, but the manner of their replacement may not have been

the same as in most sharks. The symphysial and lateral teeth in *Campodus* and *Fadenia* are not greatly different in structure. A growth series in a modern shark, *Lamna* (Fig. 3), shows the usual method of growth and replacement, the largest teeth being those that have become functional and that will presently be lost.

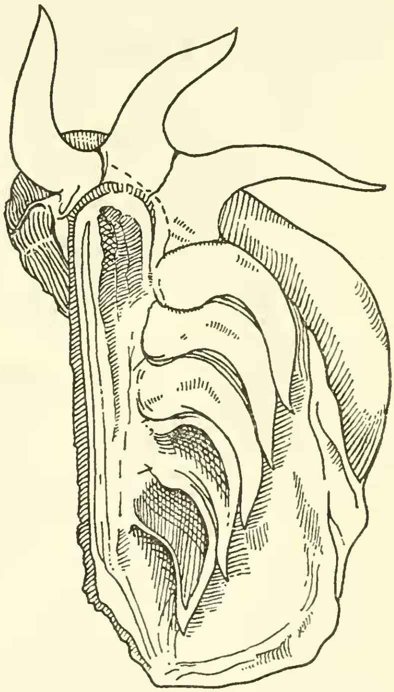

FIG. 3.—Vertical section through developing tooth-series in *Lamna*. Anterior is to left. (After Owen, from Obruchev, 1953.)

In *Edestus mirus* (Fig. 4) Hay (1912) was able to show that both the lower jaw and the upper carried symphysial teeth in long arched series; Hay also made it clear that the upper series was single, like the lower, and not paired (as erroneously stated by Nielsen, 1932:26). The lower ends of the serrated symphysial crowns in *Edestus* turn back, each being overlapped by the tooth behind it, and the osteodentinal bases are partly or completely fused into a curved bar that supports the series. Fig. 5 (Hay, 1909) shows the symphysial series of *E. crenulatus*, and Fig. 6 (Woodward, 1917) shows that of *E. newtoni*. These figures demonstrate the varying curvature of the arch in *Edestus; E. newtoni* seems most nearly to approach the spiral form.

Having established that the lower ends of the crowns, on each side of the bar, turn posteriorly beneath the following teeth, it seems that in the more extended series in *Helicoprion* (Fig. 7) the same characteristic could be used, in the absence of any associated parts of the head, to decide which way is posterior in the functional (largest) teeth of the series, provided that any close relationship exists between these two genera. Hay (1912) decided that this procedure was not acceptable because it led "to the absurd conclusion that the very small teeth of the innermost coil are the

ones that were last formed," and some other, more recent, writers have agreed. If, however, the teeth belong in the mouth and are homologous with those of *Edestus* and other sharks (which cannot be doubted), there are only two possible ways to place them in the symphysis. Either the large teeth are posterior to the sym-

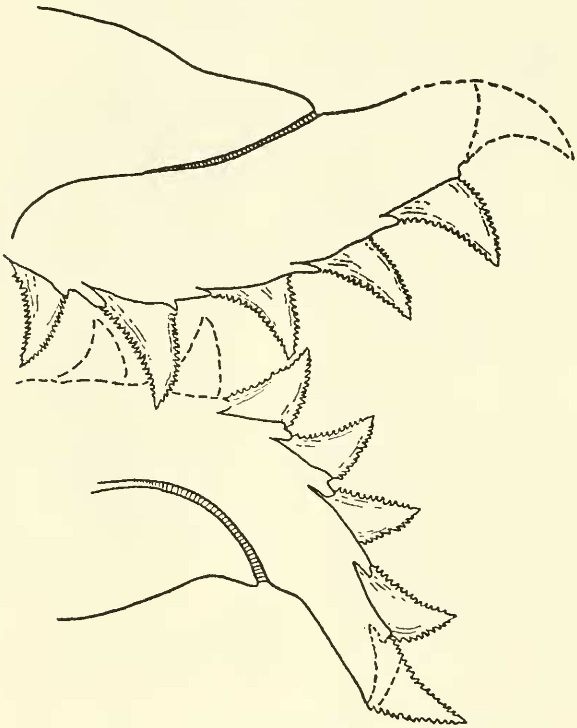

FIG. 4.—*Edestus mirus*, upper and lower symphysial teeth, right side. (After Hay, 1912.) × 0.75.

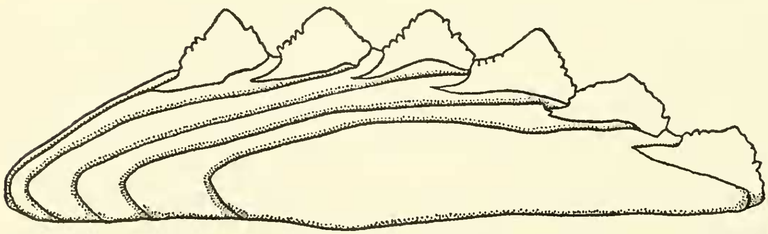

FIG. 5.—*Edestus crenulatus*, symphysial teeth, right side. (After Hay, 1909.) × 0.65.

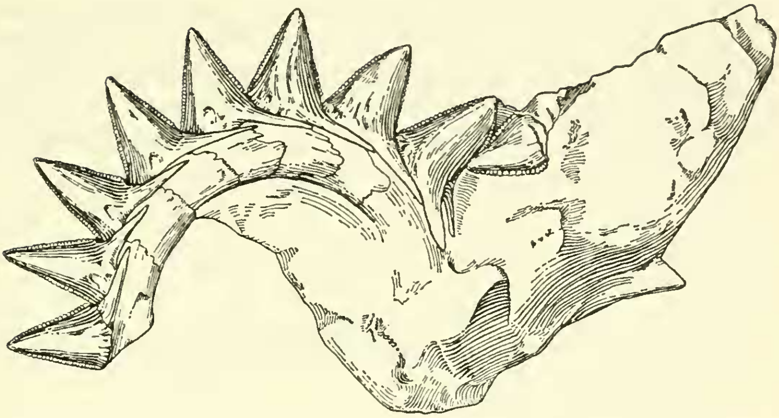

FIG. 6.—*Edestus newtoni,* symphysial teeth, left side. (After Woodward, 1917.) × 0.4.

physis, and the size decreases forward, as teeth that were formerly in use are pushed down, under and inward (the smallest teeth being oldest of all), or the large teeth are anterior, and are followed from behind by a long coiled series of replacing teeth which are still in the earlier stages of growth; in this case the smallest teeth are, indeed, those most recently formed, as is true in all known replacement series in sharks. The teeth come up and forward over the surface of the jaw from behind, and as the older, larger teeth are broken off anteriorly, those behind take their place. This concept is fully in agreement with our information on the teeth of *Edestus,* it accounts for the existence of the spiral as a growth series, and it places *Helicoprion* at the peak of specialization in the family. There is, however, some difficulty in understanding how an arched replacement series evolved into a spiral, and how it is that the youngest tooth-buds come to lie inside of two or more whorls of older teeth.

The key to both problems may lie in the fusion of the bases of the symphysial teeth into a continuous curved rod. The crowns fit against one another, even in early stages of growth, and the rod, at first small, slender, and merely arched, becomes extended as the teeth grow. A given number of teeth occupying a certain distance on the rod at an earlier stage would necessarily occupy a greater space as they grew. Pressure is therefore exerted to make the spiral grow in length, a pressure corresponding to that which

causes the movement of tooth-buds upward in the growth series of such a shark as *Lamna*. In *Helicoprion*, however, the rigidity of the growing spiral rod, formed by fusion of the basal dentine of the teeth, probably compelled an actual movement in two directions during the ontogeny of the shark (Fig. 8). Presuming

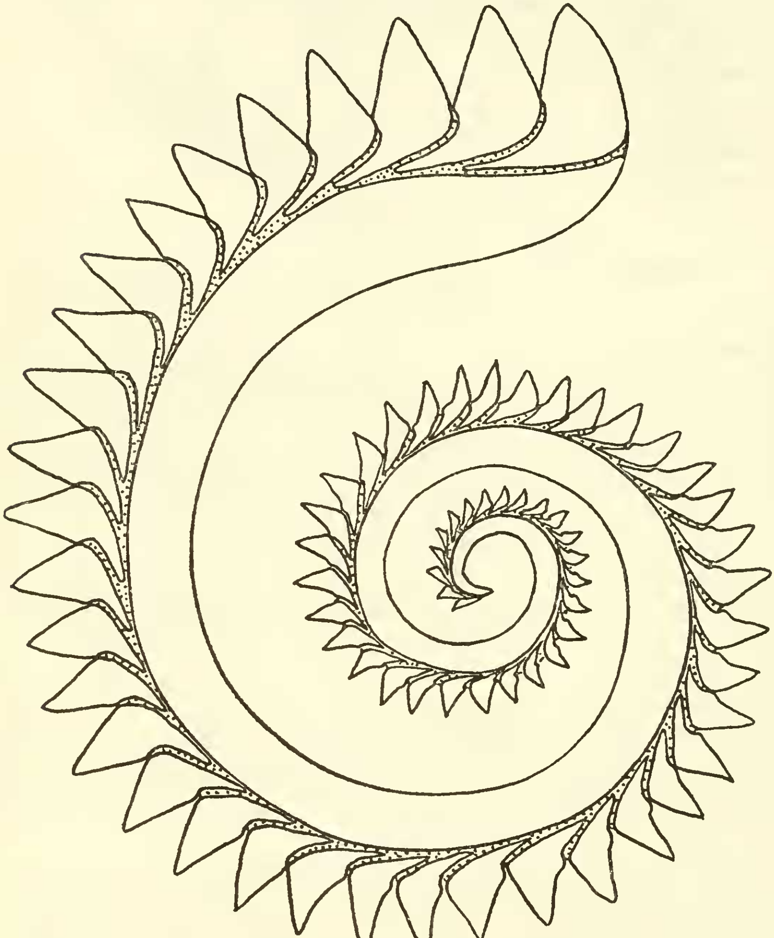

FIG. 7.—*Helicoprion ferrieri*, symphysial teeth, right side. (After Hay, 1909.) Approximately × 1.

that the first stage of formation of the symphysial tooth-row took place on the lingual, or posterior, aspect of the symphysis, as is most probable, and that the rate of growth is greatest in the

youngest individuals, the tendency of the uppermost teeth in the series to move up and forward would be equalled or exceeded by the tendency of the lower part of the series to be pressed down. Since the curvature of the symphysial surface in the youngest individuals is much greater than in older, and since the spiral rod is present upon this surface at an early age, any downward movement compels the series of younger tooth-buds to retreat inward and forward beneath the symphysis, curling eventually up and back, below the functioning row of larger teeth that stand on the occlusal surface. It appears more likely that a row of embryonic tooth-buds would retreat into the tissues of the jaw, forming in a sense a spiral pocket for their development, than that old, used

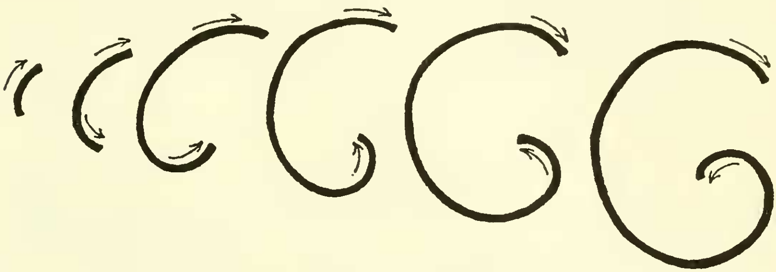

Fig. 8.—*Helicoprion.* Diagram of growth of spiral band of symphysial teeth.

teeth would be forced down into the flesh in a spiral from the anterior end of the functioning tooth-row. If growth, loss and replacement in the symphysial series were rapid, the largest teeth, here considered to have been those at the anterior margin of the jaw, would be replaced frequently as they broke off and the large end of the spiral moved outward.

Evidently in the family Edestidae the food was something that required crushing; there is little difference in the lateral teeth between one genus and another, so far as known. But evolutionary advance in the family was associated with the increasing specialization of the median tooth-series, probably in both upper and lower jaws. This implies that the feeding action involved a different use of the symphysial teeth from that of the lateral series, and in *Edestus* the form suggests a scissorlike motion of the powerful symphysial series in a vertical plane. Presumably the teeth could then be used to cut off or pull away objects growing on a surface (such as mussels, corals, hydroid clusters, stalked barnacles, and

crinoids), or, alternatively, to dig and pull out burrowing clams from mud or sand. It seems more likely that the first of these is correct, and moreover that the teeth did not have a defensive or predatory function.

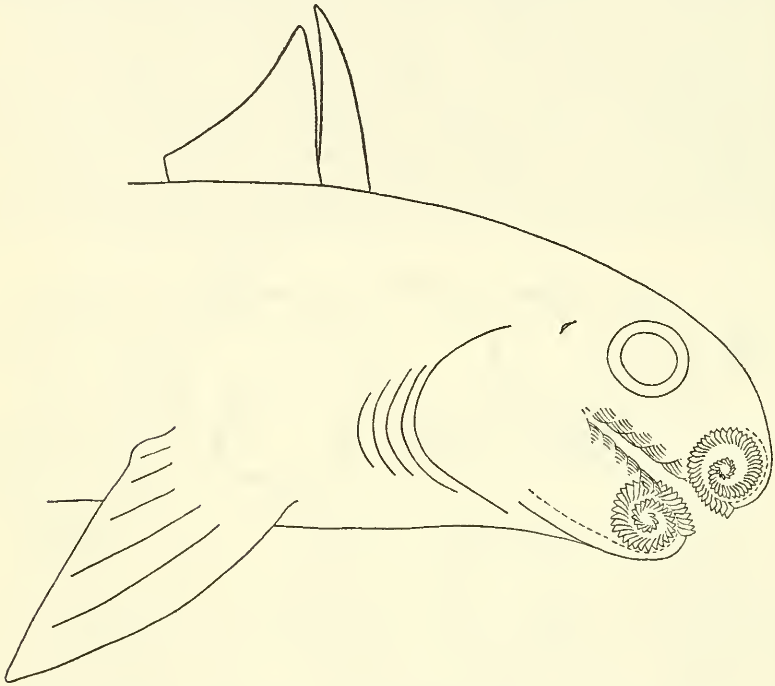

FIG. 9.—Hypothetical reconstruction of *Helicoprion*, showing symphysial teeth.

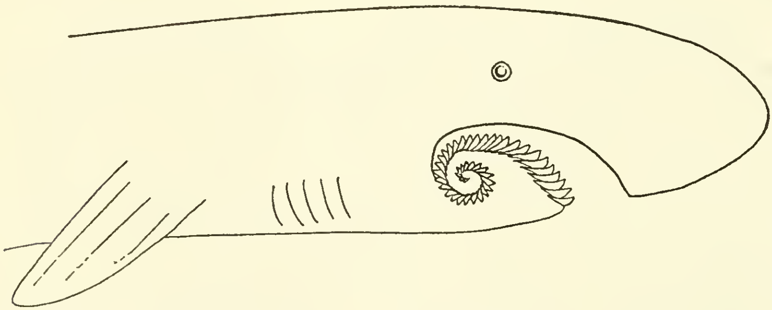

FIG. 10.—Van Den Berg's reconstruction of *Helicoprion*. (From Obruchev, 1953.)

If *Helicoprion* is the end-form of the family in a morphological sense, and if it resembled *Edestus* in having a symphysial series in the upper as well as the lower jaw, then the diagrammatic restoration in Fig. 9 suggests the possible arrangement of the teeth, the head being viewed as a transparent object. Although direct evidence is lacking, there can be little doubt that in support of a mechanism primarily for crushing shells the upper jaw must have been fused with the cranium, as in Holocephali. The only previous figure known to the writer, in which the spiral is shown with the larger teeth forward, is a sketch sent by Van Den Berg to Karpinsky in a letter dated November 21, 1899, reproduced by Obruchev, 1953, and here shown as Fig. 10. In this drawing, however, Van Den Berg appears to have regarded the tooth series as resting upon a median lower jaw, and he did not know that there were also lateral teeth. He compared the spiral to the radula of a gastropod mollusk.

LITERATURE CITED

DEKONINCK, LAURENT G.
1842-44. Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique. 2 vols. Liège.

EASTMAN, C. R.
1902. Some Carboniferous Cestraciont and Acanthodian Sharks. Bull. Mus. Comp. Zool., *39*(2): 55-99, 14 figs., 7 pls.
1903. Carboniferous fishes from the central western states. Bull. Mus. Comp. Zool., *39*(7): 163-226, 17 figs., 5 pls.

HAY, O. P.
1909. On the nature of *Edestus* and related genera, with descriptions of one new genus and three new species. Proc. U. S. Nat. Mus., *37*: 43-61, 7 figs., 4 pls.
1912. On an important specimen of *Edestus;* with description of a new species, *Edestus mirus*. Proc. U. S. Nat. Mus., *42*: 31-38, 2 pls.

LOHEST, MAXIMIN.
1884. Recherches sur les poissons des terrains paléozoiques de Belgique. Annales Soc. Geol. Belgique, *11*: 295-325, 4 text figs., 3 pls.

MOY-THOMAS, J. A.
1939. The early evolution and relationships of the elasmobranchs. Biol. Reviews, *14*: 1-26, 12 figs.

NEWBERRY, J. S., and A. H. WORTHEN.
1870. Descriptions of fossil vertebrates. In: Paleontology of Illinois. Geol. Surv. Illinois, *4*(2): 345-374.

NIELSEN, EIGIL.
1932. Permo-Carboniferous fishes from East Greenland. Meddelelser om Grønland, *86*(3): 1-63, 7 figs., 16 pls.

OBRUCHEV, DIMITRY.
1953. Study of Edestids and the works of A. P. Karpinsky. (In Russian) Trudy Paleontologicheskogo Instituta, *45*, Akademia Nauk SSSR.

RADINSKY, L.
1961. Tooth histology as a taxonomic criterion for cartilaginous fishes. Jour. Morph., *109*(1): 73-92, 2 text figs., 10 pls.

ST. JOHN, ORESTES, and A. H. WORTHEN.
1875. Descriptions of fossil fishes. In: Paleontology of Illinois. Geol. Surv. Illinois, 6(2): 247-488.

WOODWARD, A. S.
1917. A new species of *Edestus*. Quart. Jour. Geol. Soc. London, 72 (285): 1-6, 4 figs., 1 pl.
1921. Observations on some extinct elasmobranch fishes. Proc. Linn. Soc. London, sess. *133*: 20-39, 4 figs.

Transmitted June 13, 1962.

29-4226